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## CHROMOSOMES OF MEXICAN *SEDUM* III. SECTIONS CENTRIPETALIA, FRUTICISEDUM, AND OTHER WOODY SPECIES

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This is the third paper in a series reporting the chromosomes of 100 or so species of Mexican *Sedum*. A general introduction, materials and methods, and acknowledgements are included in the first paper, which dealt with 10 annual and biennial species (Uhl, 1976). A second paper reported the chromosomes of 19 more or less woody species having lateral inflorescences, considered to represent Section *Pachysedum*, plus three of their hybrids that have been named as species (Uhl, 1978).

This paper reports the chromosomes of 24 or possibly 25 additional more or less woody Mexican species that differ from Section *Pachysedum* in having terminal inflorescences. In part through the generosity of several collaborators, plants have been available from the type collections of ten species (two of them reduced to synonymy) and from at or very near the type localities of five others (including one that is reduced to synonymy). Most of the species reported here were classified by Berger (1930) in his sections *Dendrosedum*, *Fruticisedum*, and *Leptosedum*, along with several species having lateral inflorescences that appear to belong in section *Pachysedum*, reported in the preceding paper (Uhl, 1978). Clausen (1943) designated these four woody sections, plus his new section *Craigia*, as subgenus *Pachysedum*. Extensive experiments with hybridization in cultivation show that the distinction between those woody species having lateral inflorescences (Section *Pachysedum*) and those having terminal inflorescences appears to correspond to an important genetic discontinuity in the genus. In general, species of section *Pachysedum* are more easily hybridized with other species

of section *Pachyseudum* than they are with most or all of the woody species reported here, all of which have terminal inflorescences (Uhl, 1978, and unpub.). Hybrids between species with terminal inflorescences and species of section *Pachyseudum*, once obtained, are likely to be much slower to flower than are hybrids between two species of section *Pachyseudum*, and several such hybrids more than ten years old have never flowered. In particular, chromosome pairing is nearly always much more normal in hybrids between two species of section *Pachyseudum* than it is in hybrids between species of *Pachyseudum* and species with terminal inflorescences.

The woody species reported in this paper represent a much more diverse group cytologically and genetically than do the species of section *Pachyseudum* (Uhl, 1978). Choice of species to be reported here (or not) in some cases has necessarily been arbitrary, and it is likely that some of them are more closely related to some of the smaller, more "typical" species of *Sedum*, to be reported later, than they are to each other.

Among these species are several groups that are morphologically similar and that have the same or similar basic chromosome numbers. These species have been grouped here accordingly, but no new names for species or sections are introduced, since such groupings require more extensive morphological studies. This paper makes available the cytological evidence (the chromosome numbers and some information on hybrids and chromosome pairing) which is necessary to any new classification.

During these studies of the Mexican Crassulaceae several thousand crosses have been attempted, in part to establish the species that can be hybridized with each other and to note the form of their hybrids, and in particular to note the extent and manner of pairing among the chromosomes at meiosis in the hybrids. These features can be valuable indicators of the homologies among the chromosomes and of their changes during evolution. Many hybrids have been produced between species that are very different and that are widely separated taxonomically—some hybrids even have parents that, by the conventional taxonomy, are classified in different subfamilies. Many thousands of additional hybrids also might have been attempted, given enough time and space. (Some readers may be skeptical regarding certain hybrids because their parents differ so greatly and have been separated so widely in classification. However, most of the hybrids cited here have flowered, and pairing of

their chromosomes has been analyzed; color photographs of many have been made; and herbarium vouchers have been prepared. I can only invite any skeptics to inquire further.)

In discussing each species here it seems useful to mention its hybrids, even though for some species only a few crosses have been attempted. However, some caution must be exercised before drawing sweeping conclusions about relationships based upon the ability of two species to produce hybrids. Several cases are noted below of unsuccessful attempts to cross two similar, presumably closely related, species. Failure to hybridize can result from many causes, ranging from massive incompatibility because of too distant relationships to individual genes that regulate cross compatibilities, from choice of pollen or stigmas at unfavorable times or stages to unfavorable temperatures or other environmental conditions. In some cases two plants that failed to hybridize in earlier attempts may later have been successfully crossed. On the other hand, some very wide crosses might have succeeded because of plain good luck, and many efforts to duplicate them might fail.

The extent of pairing between the parental chromosomes should be a better indicator of the degree of relationship between the parents, but even this can sometimes be misleading. In several cases preparations made at different times from the same plant have shown significant differences in the amount of pairing among the chromosomes. This is probably caused by factors such as temperature or the general vigor of the plant, which seem able sometimes to affect the degree of homology that chromosomes must have in order to pair. In some hybrids, especially in those resulting from wide crosses, a wide range of pairing configurations is noted in different cells that are side by side. The natural tendency in such cases is to analyze those cells that are clearest and easiest to study, i.e., those which show the most nearly normal meiosis. Nevertheless, in spite of these hazards and reservations, it seems worth presenting here some of the information regarding hybrids and the pairing of their chromosomes.

#### SECTION CENTRIPETALIA ALEXANDER

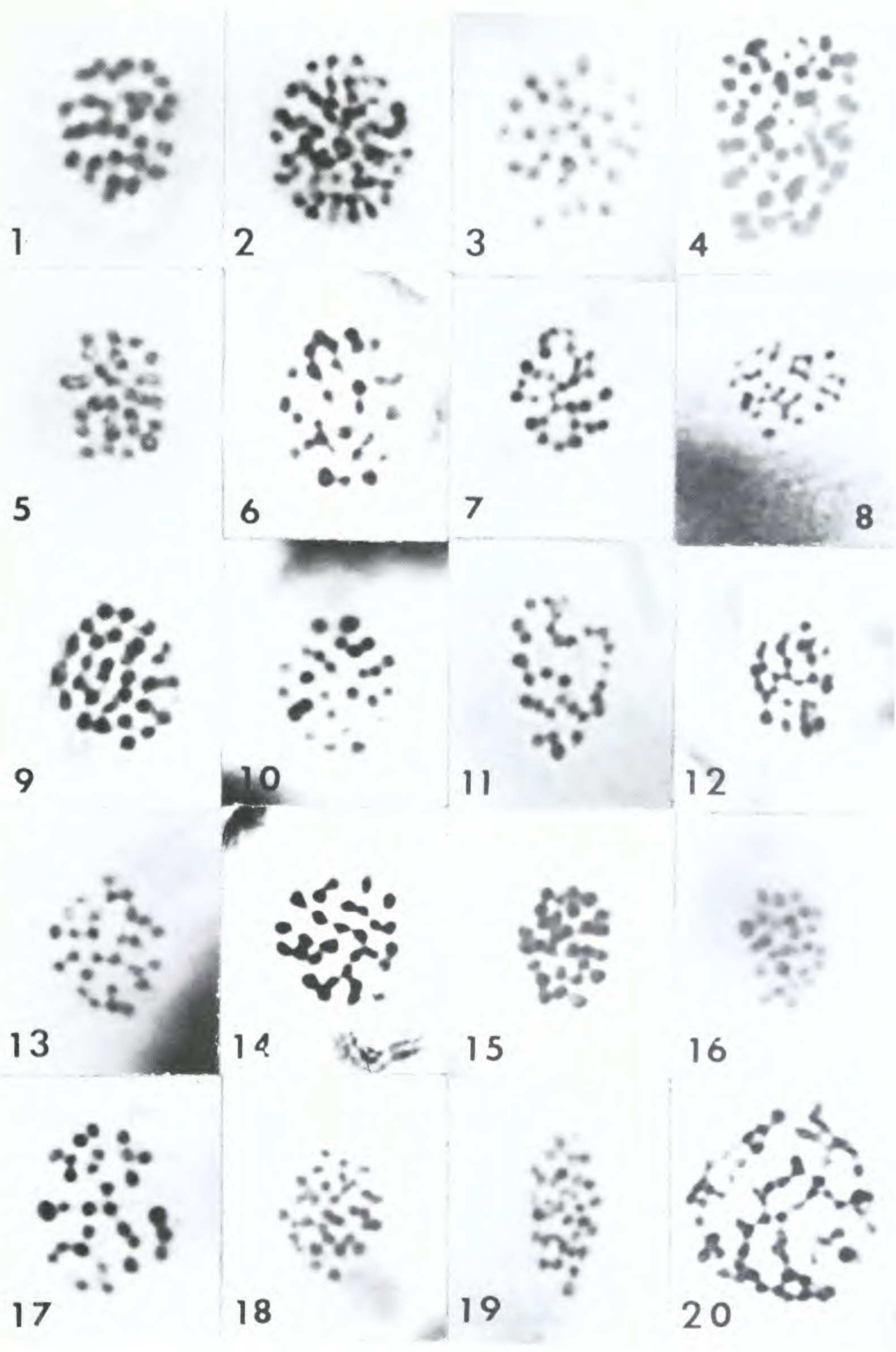
This section consists of two closely related species that are inter-fertile in cultivation, *Sedum allantoides* Rose and *S. platyphyllum* Alexander. Both species have thick leaves and they have terminal

inflorescences of a type—compound pleiochasium—that is very unusual in the Crassulaceae (Moran, 1966). The flowers are nearly identical in the two species, with separate, whitish petals that are usually marked distally (sometimes faintly) with patches of reddish brown. Somewhat similar markings occur on the petals in the genus *Graptopetalum* of Subfamily Echeverioideae, which has lateral inflorescences and sympetalous corollas. The two species of section *Centripetalia* appear to represent extremes of a morphological and genetic gradient or continuum in leaf shape, with more or less terete-leaved forms (*S. allantooides*) to the north and west, near the Puebla-Oaxaca border, flat-leaved forms up to 5 times as wide as thick (*S. platyphyllum*) 200–300 km. to the southeast, and intermediate forms (e.g., U2383) in between. Most collections, including plants of the type collections of both species, have  $n = 29$  (Fig. 1,3). One collection of *S. allantooides* obtained from cultivation in Mexico (M6358, Fig. 2) and one plant of an otherwise diploid collection of *S. platyphyllum* (M7737, Fig. 4) were tetraploids, with  $n = 58$ .

A plant of the type collection of *Graptopetalum goldii* Matuda also has  $n = 29$  (Fig. 5). This name was given to a plant with inflorescences and flowers similar to those of *Sedum allantooides* and *S. platyphyllum*, but intermediate in leaf shape, said to have been collected by Dudley Gold near Ixmiquilpan, Hidalgo. However, the locality is far removed from the ranges of the latter two species; Gold denies having collected any such plant there (Moran, 1966); and other collectors have been unable to find it there. Nevertheless, the true affinities of *G. goldii* appear to be beyond question, and Moran (1966) reduced the species to synonymy under *S. allantooides*, since that is the more variable of the two related species. In fact, U2383 appears to be a good match for *G. goldii*, which may well have come from the same locality, only a few meters from the main highway from Mexico City to Oaxaca.

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Figures 1–20. Chromosomes of *Sedum* at metaphase I in pollen mother cells,  $\times 2000$ , except as indicated. 1–2, *S. allantooides*: 1, M7724,  $n = 29$ ; 2, M6358,  $n = 58$ ; 3–4, *S. platyphyllum*, M7737; 3,  $n = 29$ ; 4,  $n = 58$ ; 5, "*Graptopetalum goldii*", M8431,  $n = 29$ ; 6, *S. platyphyllum*  $\times$  *S. allantooides*, M7737  $\times$  M7724,  $n = 29$ ; 7, *S. bourgaei*, M10155,  $n = 29$ ; 8, *S. chloropetalum*, M10096,  $n = 29$  (metaphase II); 9, *S. frutescens*, M6400,  $n = 30$ ; 10–11, *S. griseum*; 10, C44-112,  $n = 26$ ; 11, MVR-SL10,  $n = 30$ ; 12, *S. guadalajaranum*, U2322,  $n = 29$ ; 13, *S. cf. guatemalense*, U1653,  $n = 27$ ; 14, *S. oxycoccoides*, U2330,  $n = 29$ ; 15, *S. oxypetalum*, M7786,  $n = 29$ ; 16–17, *S. retusum*; 16, U1642,  $n = 27$ ; 17, U1872,  $n = 29$ ; 18, *S. obcordatum*, U1583,  $n = 34$ ; 19–20, *S. palmeri*; 19, U1367,  $n = 34$ ; 20, U1836,  $n = 68$ .



Artificial hybrids between *Sedum platyphyllum* and *S. allantooides* (M7737  $\times$  M7724) also are a good match for *Graptopetalum goldii*, show normal chromosome pairing and distribution at meiosis (Fig. 6), and are fertile. One second-generation plant, the only one studied cytologically among 65 obtained after selfing the F<sub>1</sub> hybrid, also shows mostly normal meiosis, with  $n = 29$ .

The similarities between Section *Centripetalia* and *Graptopetalum* in the fetid odor and in the markings of their petals are probably the result of convergence, possibly adaptations to pollination by carrion flies or the like. The terminal inflorescences of Section *Centripetalia* (vs. lateral inflorescences in *Graptopetalum*), the separate petals spreading from the base (vs. petals that are connate and erect at the base), the erect (vs. reflexed) stamens after anthesis, and probably the basic chromosome number ( $n = 29$  vs.  $x = 30-35$ , Uhl, 1970) argue against a close relationship between these two species and *Graptopetalum* (Moran, 1966).

Furthermore, most diploid species of *Graptopetalum* are relatively easily hybridized with each other and also with other genera of subfamily Echeverioideae, as well as with species of section *Pachysedum* of *Sedum*; and a very substantial amount of chromosome pairing occurs in nearly all such hybrids. By contrast, diploid *Sedum allantooides* and *S. platyphyllum* seem more difficult to cross with species of *Graptopetalum* (only two definite hybrids obtained in nine such attempts) and with other genera of Echeverioideae (four definite hybrids in 18 attempts) and also with species of *Sedum* section *Pachysedum* (one hybrid in nine attempts). Six of the hybrids resulting from these crosses have been studied cytologically, and their meiosis was very irregular, with analysis of chromosome pairing very difficult and usually with more univalents than paired elements at metaphase I. For example, in *S. allantooides* (M6368,  $n = 29$ )  $\times$  *Graptopetalum fruticosum* (U1078,  $n = 31$ ) only three cells could be analyzed at metaphase I; these had 16-19 bi- and multi-valents and 22-28 univalents. *Sedum platyphyllum* (M7737,  $n = 29$ )  $\times$  *S. cremnophila* of section *Pachysedum* (M10174,  $n = 33$ ) showed 16-26 bi- and multi-valents and 7-27 univalents in 12 cells analyzed at metaphase I (Uhl, 1976a), with numerous laggards and 3 or more bridges at anaphase I and mostly abnormal-appearing microspores. Hybrids of *Sedum allantooides* with *Echeveria nodulosa* ( $n = 16$ ) and of *S. platyphyllum* with *E. ciliata* ( $n = 25$ ) and with *Pachyphytum hookeri* ( $n = 32$ ) are about as irregular at meio-

sis. Thus the genomes of the two species of Section *Centripetalia* appear to be organized very similarly to each other but very differently from those of *Graptopetalum* and other genera of subfamily Echeverioideae and also from those of *Sedum*, section *Pachysedum*. Relatively little chromosome pairing was seen also in three other hybrids between *S. platyphyllum* ( $n = 29$ ) and two additional species belonging to other groups of *Sedum* (*S. stahlii* and *S. greggii*).

The best chromosome pairing noted in any hybrid of either species of Section *Centripetalia* with any outside species occurred in *Sedum platyphyllum* ( $n = 29$ )  $\times$  *S. obcordatum* ( $n = 34$ ) (M7737  $\times$  U1583), where 27–29 bi- and multi-valents and 0–4 univalents were noted in 15 cells analyzed, and mostly normal-looking microspore quartets were seen. This was unexpected, because the parental species are quite different both morphologically and in their chromosome numbers and seem not closely related.

The relatively poor chromosome pairing seen in most of the hybrids cited above means that the chromosomes of *Sedum allantooides* and *S. platyphyllum* probably have relatively little homology for those of most other species of *Sedum* and the other genera; this provides genetic support for Moran's (1966) conclusion that the two species of section *Centripetalia* are morphologically distinct from other species and should be maintained as a separate group. (*Sedum platyphyllum*  $\times$  *S. obcordatum* is the lone exception to the rule of poor pairing in these hybrids, but, as noted, the latter species otherwise seems not closely related.)

The very limited chromosome pairing in most of these hybrids also means that few or none of the 29 chromosomes contributed to a hybrid by *Sedum allantooides* or by *S. platyphyllum* have enough homology with any of the 28 other chromosomes from the same parent that they can pair with each other. Thus, in spite of their relatively high basic chromosome numbers ( $n = 29$ ), *S. allantooides* and *S. platyphyllum* are regarded here as effectively diploid now, regardless of how they may have originated. The same kind of evidence has argued for relatively high basic chromosome numbers in other groups of Mexican Crassulaceae:  $x = 30$ – $34$  in *Sedum* section *Pachysedum* (Uhl, 1978) and also in *Graptopetalum* (Uhl, 1970),  $x = 31$ – $33$  in *Pachyphytum* (Uhl & Moran, 1973),  $x = 33$  in *Sedum cremnophila* and its relatives (Uhl, 1976a).

Fertile hybrids have been produced in the Mexican Crassulaceae from crosses between a number of very different pairs of tetraploid

parents, some belonging to different genera (Uhl, unpublished). These hybrids show normal, or nearly normal, pairing of their chromosomes at meiosis, apparently because the two sets of chromosomes that the hybrid received from each parent regularly pair with other other (autosyndesis). This allows a balanced distribution of the chromosomes to the reproductive cells, some of which are functional even in some intergeneric hybrids. The extensive, often apparently complete, autosyndesis means that the parents are autotetraploid.

One collection of *Sedum allantoides* appears to be such an autotetraploid (M6358,  $n = 58$ ). A hybrid of this with the diminutive *S. compactum* ( $n = 60$ , probably) has nearly normal meiosis, with 59 bivalents in many cells, and it produces quartets and microspores that appear normal and 10.2% pollen that is stainable in aniline blue-lactophenol. Ten second-generation hybrids were grown from seed produced spontaneously by the  $F_1$  hybrid. The presumed formation of 29 bivalents by autosyndesis among the 58 chromosomes that this hybrid received from tetraploid *S. allantoides* (M6358) contrasts sharply with the apparent inability of any of the 29 chromosomes contributed to other hybrids by other collections of the same species to pair with each other, and it strongly reinforces the conclusion above that the plants of *S. allantoides* with  $n = 29$  are effectively diploid. Tetraploid *S. allantoides* has also been crossed with tetraploid collections of *Graptopetalum macdougallii* ( $n = 66$ ), *G. saxifragoides* ( $n = 64$ ), and *Echeveria secunda* ( $n = 30 \pm$ ).

#### SECTION FRUTICISEDUM BERGER

A second probably natural group is listed here as section *Fruticisedum* Berger. Ten shrubby and subshrubby species of this section, as it is interpreted here, have been studied. The leaves are linear or thin and mostly narrow, and the flowers mostly white or pale pinkish. All of these species have  $n = 26$  to  $n = 31$  or a multiple, and six of them have  $n = 29$ . Five of these species (*Sedum chloropetalum*, *S. frutescens*, *S. oxypetalum*, *S. pulvinatum*, and *S. retusum*) were listed under section "*Frutisedum*" by Jacobsen (1974); three others (*S. bourgaei*, *S. griseum*, and *S. guadalajaranum*) were under section *Leptosedum* (which is here merged); one (*S. guatemalense*) was listed under section *Pachyseudum*, and one (*S. oxycoccoides*) as a "true" *Sedum*. Of additional species listed in



*Frutisedum* by Jacobsen, *S. amecamecanum* is a natural hybrid of *S. praealtum* with *Villadia batesii* (Clausen, 1959; Uhl, 1978), *S. conzattii* was not available, *S. cuspidatum* ( $n = 34$ ) and *S. hultenii* ( $n = 26$ ) have lateral inflorescences and belong to section *Pachyseudum* (Uhl, 1978), and *S. quevae* ( $n = 20$  and  $21$ ), *S. tortuosum* ( $n = 15$  and  $16$ ) and *S. tuberculatum* ( $n = 16$ ) differ cytologically from the others and probably are not closely related to them.

Six species of this section have the same chromosome number ( $n = 29$ ) as the two species of section *Centripetalia*, but only two crosses between the two groups have been attempted, both unsuccessful, and nothing is known of homologies between their chromosomes.

Some species of *Villadia* subgenus *Altamiranoa* (e.g., *V. batesii*,  $n = 25$ , and *V. elongata*,  $n = 23$ ) are very similar in general habit and in other characters to some species of section *Fruticisedum* (e.g., *Sedum bourgaei*), differing chiefly in their basally erect and connate corollas, which are approached by several species of this section. It seems likely that *Villadia*, or at least its subgenus *Altamiranoa*, may have been derived from a common ancestor with section *Fruticisedum*.

*Sedum bourgaei* Hemsley ( $n = 29$  in eight collections from seven localities, Fig. 7) is a subshrub with reddish brown stems, linear leaves, and white flowers. It occurs from near Mexico City west into central Michoacan and north to southern Queretaro (Clausen, 1959). Although Berger (1930) and Jacobsen (1974) classified it in a different section, in many respects the species seems both morphologically and geographically to occupy a central position in section *Fruticisedum*, and some of the other species are easily characterized by how they differ from it: *S. chloropetalum* by its lanky stems and green flowers, *S. frutescens* by its large size and massive stems, *S. griseum* by its somewhat thicker, grayish stems with peeling bark, *S. guadalajaranum* by its tubers and more delicate leaves, *S. oxycoccoides* by its deep red flowers, *S. oxypetalum* by its massive stems and broader leaves, and *S. retusum* by its broader leaves with retuse tips. A hybrid between *S. bourgaei* and the diminutive *S. greggii* ( $n = 26$ ) (U1535  $\times$  M10155) showed very little chromosome pairing at meiosis. Attempted crosses with *S. palmeri*, *S. platyphyllum*, and *S. quevae* were unsuccessful.

*Sedum chloropetalum* Clausen ( $n = 29$  in two collections, including the type, from two localities, Fig. 8) resembles *S. retusum* but

grows taller and differs conspicuously in its rounded leaf apices and yellowish green petals. The species is native in the Sierra Madre del Sur of southeastern Oaxaca. No hybrids have been produced in two attempts.

*Sedum frutescens* Rose ( $n = 30$  in five collections from three localities, Fig. 9) resembles *S. oxypetalum* in its large size (up to a meter or more in height), thick stems (up to 10 cm. or more in diameter at the base), and exfoliating bark. It differs from the latter in its white (vs. pinkish) flowers and longer, narrower leaves and in its time of flowering (dry season—winter and spring—often when leafless or nearly so, vs. wet season—summer—for *S. oxypetalum*). The chromosome number ( $n = 30$ ) also differs consistently from that in *S. oxypetalum* ( $n = 29$ ). *Sedum frutescens* has been crossed with two species of subfamily Echeverioideae, *Graptopetalum fruticosum* ( $n = 31$ ) and *Pachyphytum hookeri* ( $n = 32$ ). The latter hybrid has flowered and shows very irregular meiosis, as expected, with relatively poor chromosome pairing. Attempted crosses with *S. cremnophila* and *S. torulosum* were unsuccessful.

*Sedum griseum* Praeger, as here reported, consists of two morphological and cytological forms. Populations from Guanajuato, and possibly also from Queretaro, have grayish, glaucous leaves and  $n = 26$  (in nine collections from five localities, Fig. 10). Plants from farther south, in Jalisco and Michoacan, are greener and differ in other characters and all have  $n = 30$  (seven collections from five localities, Fig. 11). The type collection originated in Mexico without further information as to locality, but Clausen (1959) considered that a cultivated plant like those reported here from Guanajuato with  $n = 26$  was a closer match for the type than those from farther south. However, he concluded from his morphological studies that both forms should be kept in the same species, possibly as separate subspecies. The consistent difference in chromosome numbers, with no intermediate numbers known, and also the disjunct distributions indicate that a significant separation into at least incipient species has occurred between these two. Possibly a reexamination of their morphological differences might justify their recognition as separate species. *Sedum griseum* is most likely to be confused with *S. bourgaei* (Clausen, 1959), but the latter species consistently has  $n = 29$ . *Sedum griseum* has been crossed with the diminutive *S. greggii* ( $n = 26$ ), but 11 other crosses (five of them with species of *Villadia*) yielded nothing.

## Table 1. Chromosome numbers.

Section *Centripetalia* Alexander***Sedum allantoides* Rose ( $n = 29$ )**

*U1200* Type collection. Puebla: Hills near San Luis Atolotitlan, 2000–2100 m. (J. N. Rose 07/471 via Univ. Mich. Bot. Garden 9369).

*M7724* (Figure 1) Topotype (R. Moran).

*U1456*, *M6368* Oaxaca: Rocks above Mex. 125 at S. edge of Miltepec, 1900 m. (C. H. Uhl, R. Moran).

*U2383* Oaxaca: Small cliffs along Mex. 190 at Km. 32.3 SE of Huajuapán, ca. 6 km. N. of Tamazulapán, 1900 m.

*U1207*, *M3209*, *C47-11* All cultivated.

*M8431* (Figure 5) Type collection of *Graptopetalum goldii* Matuda. Cultivated.

***Sedum allantoides* Rose ( $n = 58$ )**

*M6358* (Figure 2) Cultivated: San Antonio Texcala, Puebla (R. Moran).

***Sedum platyphyllum* Alexander ( $n = 29$ )**

*M7737* Oaxaca: 6 km. NW of Totolapán, 1300 m., shaded cliff (R. Moran) (One plant had  $n = 29$ , Figure 3, another  $n = 58$ , Figure 4)

*M10143* Oaxaca: El Convento, near Portillo Nejapa, ca. 1500 m. (T. MacDougall, via R. Moran).

*M11808* Oaxaca: Cerro San Pedro, Tehuantepec, 1150 m. (T. MacDougall, via R. Moran).

*C42-7*, *C47-40* Type collection. Oaxaca: Cerro Guiengola, near Tehuantepec (T. MacDougall, via R. T. Clausen).

Section *Fruticisedum* Berger***Sedum bourgaei* Hemsley ( $n = 29$ )**

*C48-39* Michoacán: pine-oak woods 8 km. S. of Patzcuaro, 2300 m. (R. T. Clausen).

*U2261* Michoacán: Cliffs along Mex. 15 at Km 190.8 (W. of Toluca), 2.4 km. W. of Puerto Garnica (summit of Sierra de Ozumatlan), 2850 m.

*U1414*, *Z-Z3* Michoacán: Rocks along Mex. 15, 20 km. E. of Zitacuaro, 2600 m. (C. H. Uhl, R. T. Clausen).

*M10149* State of Mexico: Amanalco, 2300 m. (R. Moran).

*M10155* (Figure 7) State of Mexico: 11 km. E. of Temascaltepec, 2150 m. (R. Moran).

*U2515* State of Mexico: 14 km. NE of Temascaltepec, 2320 m.

*U2512* State of Mexico: 5 km. NE of Meson Viejo, 3200 m.

***Sedum chloropetalum* Clausen ( $n = 29$ )**

*M10096* (Figure 8) Oaxaca: Portillo de Zeta (R. Moran).

*C45-50* Type collection. Oaxaca: Santo Tomas Teipa, SW of Tehuantepec (ca. 16° 20'N, 95° 35'W) (T. MacDougall, via R. T. Clausen).

***Sedum frutescens* Rose ( $n = 30$ )**

*U2022*, *U2067* State of Mexico: Above Santo Tomas hydroelectric plant, W. of Valle de Bravo (Jay Dodson 471).

*U1431, M6400* (Figure 9) Near topotypes. Morelos: Pedregal above Cuernavaca (C. H. Uhl, R. Moran).

*U1446* Guerrero: 1 km. E. of east entrance to Taxco, Mex. 95.

***Sedum griseum* Praeger ( $n = 26$ )**

*U2475* Guanajuato: Near San Felipe, 1800 m. (F. Otero).

*U2116, M14729* Guanajuato: Pichachos de la Bufa, on NE side of Guanajuato, 2300 m. (C. H. Uhl, R. Moran).

*U2272, M10193* Guanajuato: Sierra de Guanajuato, 3.3 km. SW of Mesa San Jose & 32 km. SW of Dolores Hidalgo, 2350 m. (C. H. Uhl, R. Moran).

*C49-3* Guanajuato: E. of San Luis de la Paz (C. L. Gilly 131, via R. T. Clausen).

*C44-111* Queretaro: San Juan del Rio (J. N. Rose #05/120, N.Y. Bot Garden 24066, via R. T. Clausen).

*C44-112* (Figure 10), *C47-32* Cultivated (R. T. Clausen).

***Sedum griseum* Praeger ( $n = 30$ )**

*U2061* Jalisco: Below La Joya, N. slope of Nevado de Colima, 2300 m. (F. C. Boutin & F. K. Brandt 2375).

*U1403, MVR-SL* (2 plants, Figure 11) Michoacan: SW of San Lorenzo on lava, ca. 20 km. N. of Uruapan. (C. H. Uhl, R. T. Clausen).

*U837, MVR-SO* (3 plants) Michoacan: Sierra de Ozumatlan, near Las Trojes, 35 km. E. of Morelia, 2320 m. (H. E. Moore, Jr., R. T. Clausen).

*U1413* Michoacan: E. side of Puente Rio Turundeo, Mex., 15, 8.4 km. N. of Tuxpan, 1825 m.

*U1425* State of Mexico: W. side of Lake Valle de Bravo.

***Sedum guadalajaranum* Watson ssp. *viridifolium* Clausen ( $n = 29$ )**

*U2322* (Figure 12) Zacatecas: 24 km. SW of Valparaiso, 2275 m. (M. Kimnach & H. Sanchez-Mejorada).

***Sedum* cf. *guatemalense* Hemsley ( $n = 27$ )**

*U1653* (Figure 13) Oaxaca: Epiphytic on oak in cloud forest near Cerro Pelón, N. of Oaxaca at Km. 129 on Mex. 175, 2820 m. (W. Handlos 370A).

***Sedum oxycoccoides* Rose ( $n = 29$ )**

*U2330* (Figure 14) Nayarit: 24 km. SW of San Juan Capistrano, Zac., on road to Jesus Maria, Nay., 2675 m. (M. Kimnach & H. Sanchez-Mejorada 1892).

***Sedum oxypetalum* H.B.K. ( $n = 29$ )**

*M7786* (Figure 15) Hidalgo: above Velasco (escaped?). (R. Moran.)

*U1417* State of Mexico: summit of hill on N. side of Toluca, 2700 m.

*U1287, M6402* Morelos: on lava flow 3 km. S. of summit of highway N. of Cuernavaca. (M. Kimnach, R. Moran).

*M3281* Cultivated.

***Sedum pulvinatum* Clausen ( $n = \text{ca. } 54$ )**

*C45-46* Type collection. Oaxaca: mountains E. of Ayutla. (W. H. Camp 2835, via R. T. Clausen).

***Sedum retusum* (Hemsley) ( $n = 27$ )**

*C7452, U1642* (Figure 16) San Luis Potosi: Sierra de Alvarez, ca. 36 km. E. of San Luis Potosi & 2 km. W. of Puerto Altamira summit, 2250 m. (R. T.

Clausen, W. Handlos 301).

*M10005*, *M13374* Near topotypes. San Luis Potosi: Sierra de Alvarez, S. and above Puerto Altamira summit, 2600 m. (Both  $n = 27 + 1$ ) (R. Moran & C. H. Uhl).

*U486*, *C43-74* Cultivated.

***Sedum retusum* Hemsley** ( $n = 28-31$ )

*C7416* Tamaulipas: Ca. 9 km. NW of Gomez Farias (R. T. Clausen). ( $n = 28+1$ ).

*U1872* (Figure 17) Hidalgo: on limestone 19 km. S. of Jacala & 1 km. S. of Minas Viejas, at Km. 79 on Mex. 85, 2050 m. ( $n = 29$ ).

*M7811* (Figure 35) Hidalgo: 21 km. S. of Jacala at El Salto ( $n = 31+1+1B$ ). (R. Moran).

*Sedum palmeri* Group.

***Sedum obcordatum* Clausen** ( $n = 34$ )

*U1583* (Figure 18) Veracruz: Barranca de Mala Cara, on SE slope of Orizaba, 4200 m. (R. T. Clausen).

***Sedum palmeri* S. Watson** ( $n = 34$ )

*C7596* Nuevo Leon: Villa de Garcia (R. T. Clausen).

*U1367* (Figure 19) Near topotype. Nuevo Leon: along road to Chipinque Mesa, SW of Monterrey, 600 m.

*C7568* Nuevo Leon: Saddle Mountain, SE of Monterrey (R. T. Clausen).

*C7545* Nuevo Leon: Near Villa Santiago (R. T. Clausen).

*U1940*, *U2084* Nuevo Leon: 24 km. W. of Mex. 85 on road to Rayones, 650 m. (M. Kimnach, C. Glass).

*U1918* Nuevo Leon: Santa Rosa Canyon, 7 km. E. of Iturbide, 1200 m.

*U2575* Tamaulipas: La Reforma (A. Lau #052).

*U120*, *C47-80* Cultivated.

***Sedum palmeri* S. Watson** ( $n = 35$ )

*U2075* Nuevo Leon: 1 km. S. of Grutas de Garcia, 850 m. (M. Kimnach 1383).

***Sedum palmeri* S. Wats.** ( $n = 68$ ) (= *S. compressum* Rose)

*U1836* (Figure 20), *C7375* Tamaulipas: Canyon 14-16 km. SW of Ciudad Victoria (C. H. Uhl, R. T. Clausen).

*C7371* Topotype of *S. compressum* Rose. Tamaulipas: Canyon SW of Ciudad Victoria (R. T. Clausen).

*C7389* Tamaulipas: Canyon W. of Ciudad Victoria (R. T. Clausen).

*U1837* Tamaulipas: Limestone along Mex. 101, 27 km. SW of Ciudad Victoria.

*U2030*, *U2153*, *U2478* Cultivated.

*C47-79* Cultivated. N. Y. Botanical Garden (via R. T. Clausen). Believed to be from the type collection of *S. compressum* Rose.

***Sedum* sp. aff. *palmeri*** ( $n = 34$ )

*M7658* (Figure 21) San Luis Potosi: Zaragoza, in the Sierra de Alvarez ( $n = 34 + 3B$ ) (R. Moran).

*M14756* Guanajuato: 16 km. E. of San Luis de la Paz (R. Moran).

***Sedum torulosum*** Clausen ( $n = 34$ )

UC54.234 (Figure 22) Same clone as the type collection. Cultivated (H. Rush, via Univ. of Calif. Bot. Garden, Berkeley).

Miscellaneous species.

***Sedum botteri*** Hemsley ( $n = 24$ )

6A (Figure 23) Veracruz: Barranca de Cuautilla, 10 km. NW of Huatusco (R. T. Clausen).

M10153½ Chiapas: El Triunfo (T. MacDougall, via R. Moran).

UC58.832 Chiapas: El Rosario, Motozintla, 2100 m. Epiphytic. (T. MacDougall B-205).

***Sedum burrito*** Moran ( $n = 34+1$ )

U2446 Type collection. Cultivated: Coatepec, Veracruz, via P. C. Hutchison, Tropic World, Inc., 1328A.

U2073 (Figure 24) Cultivated: Guadalajara, Jalisco (F. Boutin & M. Kimnach 3221).

***Sedum calcicola*** Robinson & Greenman ( $n = 32$ )

U1941, U2081 Nuevo Leon: Rayones Canyon, 20 km. W. of Mex. 85, 600 m. (C. Glass & R. Foster 3282, M. Kimnach 1393).

U2079 Nuevo Leon: 9 km. E. of Rayones, 825 m. (M. Kimnach 1411).

U832 Tamaulipas: 8 km. before Huisachol on road from Ciudad Victoria to Jaumave. (H. E. Moore, Jr. 8005).

M13368 (Figure 25) San Luis Potosi: Rocky river bank at E. side of Ocampo (formerly Bagre), ca. 16 km. WNW of Cañada Verde (R. Moran & C. H. Uhl).

U1646 Near Topotype. San Luis Potosi: S. of Las Canoas (W. Handlos 303A).

***Sedum calcicola*** Robinson & Greenman ( $n = 48$ )

U1839, M7816 (Figure 26) San Luis Potosi: 2 km. W. of Santo Domingo on Mex. 80, 18 km. E. of Mex 57 (C. H. Uhl, R. Moran).

***Sedum calcicola*** Robinson & Greenman ( $n = 64$ )

U1370 Near topotype of *S. lenophylloides* Rose. Nuevo Leon: Chipinque Mesa, SW of Monterrey.

U1529 San Luis Potosi: S. side Rio Verde 3 km. WNW of Cañada Verde.

M10046 (Figure 27) Hidalgo: Barranca de Toliman (R. Moran).

C47-16, C47-56 Cultivated (R. T. Clausen).

***Sedum furfuraceum*** Moran ( $n = 34$ )

M7659 (Figure 28) Type collection. San Luis Potosi: 18 km. SE of Zaragoza, Sierra de Alvarez, 2100 m. 21° 59'N., 100° 42'W. (R. Moran).

***Sedum morganianum*** Walther ( $n = 35$ )

UC54.419 Probably from type collection. Cultivated: Dr. Meredith Morgan.

U1270 (Figure 29), and "unnumbered" (fixed buds only, no voucher). Cultivated.

***Sedum quevae*** Hamet ( $n = 20$ )

U1289 Morelos: km. 9 on road from Cuernavaca to Tepoztlan (M. Kimnach).

SB1C Tlaxcala: 1 km. SW of San Bernabé & 6 km. NE of Tlaxcala (R. T.

Clausen).

SE3 (Figure 30) Tlaxcala: 2 km. NE of San Bernabé (R. T. Clausen).

C7496 Tlaxcala: Santa Maria Atlihuitzia (R. T. Clausen).

**Sedum quevae** Hamet ( $n = 21$ )

U2377 Oaxaca: ½ km. S. of El Estudiante & 12 km. N. of junction Mex. 190 at Oaxaca. Sierra de Juarez.

M7767 (Figure 31) Oaxaca: Ixtepec. (R. Moran).

**Sedum stahlii** Solms ( $n = 29$ )

U1460 Puebla: 2½ km. S. of Cumbres de Acultzingo, Ver.

M7774 Veracruz: El Paraje (R. Moran).

M2129 (Figure 32), M3250, UC54.169 Cultivated.

**Sedum tortuosum** Hemsley ( $n = 15$ )

M7759 Oaxaca: Portillo San Andres (R. Moran).

M10127 Oaxaca: Cerro San Felipe (R. Moran).

UC58.830 (Figure 33) Oaxaca: Cerro Madreña, Santo Tomas Quieri, 2100 m. (T. MacDougall B-203).

**Sedum tortuosum** Hemsley ( $n = 16$ )

M7620 (Figure 34) Durango: Los Angeles, 5½ km. E. of Revolcaderos (R. Moran).

U2063 Jalisco: Sierra de Minatitlan, above Haceradero, 1800 m. (F. C. Boutin & F. K. Brandt 2496).

**Sedum tuberculatum** Rose ( $n = 16$ )

C47-54 Oaxaca: Sierra de Miahuatlan (from R. T. Clausen).

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*Sedum guadalajaranum* Watson ( $n = 29$ , one collection, Fig. 12) appears like a more delicate version of *S. bourgaei* ( $n = 29$ ), with generally smaller leaves and tuberous roots. The plant studied belongs to the recently described subspecies *viridifolium* Clausen (1978). Tuberous roots also occur in some populations of *S. bourgaei*. *Sedum guadalajaranum* occurs at several localities from Guadalajara north almost to Aguascalientes (Clausen, 1978), all localities well to the northwest of the range of *S. bourgaei*. A recent cross with *S. oxycoccoides* yielded five seedlings which died before their hybrid nature could be established. An attempted cross with *S. oxypetalum* was unsuccessful.

The plant listed here as *Sedum* cf. *guatemalense* Hemsl. ( $n = 27$ , one collection, Fig. 13) was a short subshrub, epiphytic on oak in a cloud forest in northern Oaxaca. The leaves were shiny green, 1 mm. thick, 3 mm. wide, and up to 12 mm. long, with a longitudinal groove above leading to a slightly retuse tip. The corolla was yellowish, with numerous small reddish streaks, especially toward the base. If this plant is not *S. guatemalense* it is probably an unnamed

species. Authentic *S. guatemalense* (U2491), recently collected in Guatemala, is vegetatively rather similar to this, but it has not yet flowered. Of the other species, this plant seems perhaps closest to *S. retusum*, several collections of which also have  $n = 27$ . The plants later named as *S. rubrotinctum* Clausen were earlier thought to be *S. guatemalense*, an error that still persists in some collections, but they differ in many characters (Clausen, 1948b).

*Sedum oxycoccoides* Rose ( $n = 29$  in one collection, Fig. 14) also resembles *S. bourgaei* but has flowers that are deep red in color. It occurs in the Sierra Madre Occidental in the state of Nayarit and probably also in Zacatecas. Seedlings have resulted from recent crosses with *S. griseum* ( $n = 26$ ), *S. guadalajaranum*, *S. quevae* ( $n = 21$ ), and *Pachyphytum hookeri*, but an attempted cross with *S. oxypetalum* was unsuccessful.

*Sedum oxypetalum* H.B.K. ( $n = 29$  in five collections from three localities, Fig. 15) is a large species with deciduous leaves, massive stems up to 12 cm. in diameter at the base, and peeling bark. It closely resembles *S. frutescens* ( $n = 30$ ) with which it sometimes occurs, but its leaves are broader and it flowers during the wet season (summer). *Sedum frutescens* flowers during the dry season (winter), often when leafless. The difference in chromosome number appears consistent. *Sedum oxypetalum* occurs from the eastern part of the state of Mexico to central Michoacan (Clausen, 1959), often on lava. Recently a single seedling has resulted from a cross with *S. griseum* ( $n = 26$ ), but attempted crosses with *S. guadalajaranum*, *S. oxycoccoides*, *S. retusum*, and *Pachyphytum hookeri* have been unsuccessful.

*Sedum pulvinatum* Clausen ( $n = \text{ca. } 54$  in the type collection) of central Oaxaca has solitary white flowers. Clausen (1948a) classified it in Section *Fruticisedum*, which he redefined to include also Section *Dendrosedum*. He thought it closest to the yellow-flowered *S. luteoviride*, but that species appears to be a natural hybrid, *S. praealtum*  $\times$  *S. greggii* (Uhl, 1978). In terms of the chromosome numbers in the other species of this section, *S. pulvinatum* appears to be a tetraploid.

*Sedum retusum* Hemsley has relatively broad leaves (up to 6 mm.) that are often subspatulate and retuse, white petals that are often pink at the base, and pink carpels. It resembles *S. oxypetalum*, to which Fröderström (1935) considered it closely allied, but it never develops the massive stems of the latter species. Four collections



from near the type locality (Alvarez, San Luis Potosi) had  $n = 27$  (Fig. 16) (two of them trisomic), as did two other plants from cultivation. However, three other collections from farther east, in the Sierra Madre Oriental of southern Tamaulipas and Hidalgo, had  $n = 28 + 1$ ,  $n = 29$  (Fig. 17), and  $n = 31$  plus an extra chromosome of standard size and also a small B-chromosome (Fig. 35). An attempted cross with *S. oxypetalum* was unsuccessful, as were also crosses with 14 other species. However, unlikely as it seems, *S. retusum* has been hybridized with *Pachyphytum hookeri* of subfamily Echeverioideae, but the hybrid shows very little chromosome pairing.

#### SEDUM PALMERI GROUP

A third possibly natural group is referred to here as the *Sedum palmeri* group. It consists of at least three, and possibly four, subshrubby species with rather broad, glaucous leaves and yellow flowers, all with  $n = 34$  (or  $n = 68$ ). Jacobsen (1974) listed *S. palmeri*, *S. compressum* (here considered to be no more than a tetraploid subspecies of *S. palmeri*), and *S. torulosum* in his section *Dendrosedum*, and he classified *S. obcordatum* as a "true" *Sedum*. From their vegetative appearance and chromosome numbers these species might be classified in section *Pachysedum*, but they all have terminal inflorescences.

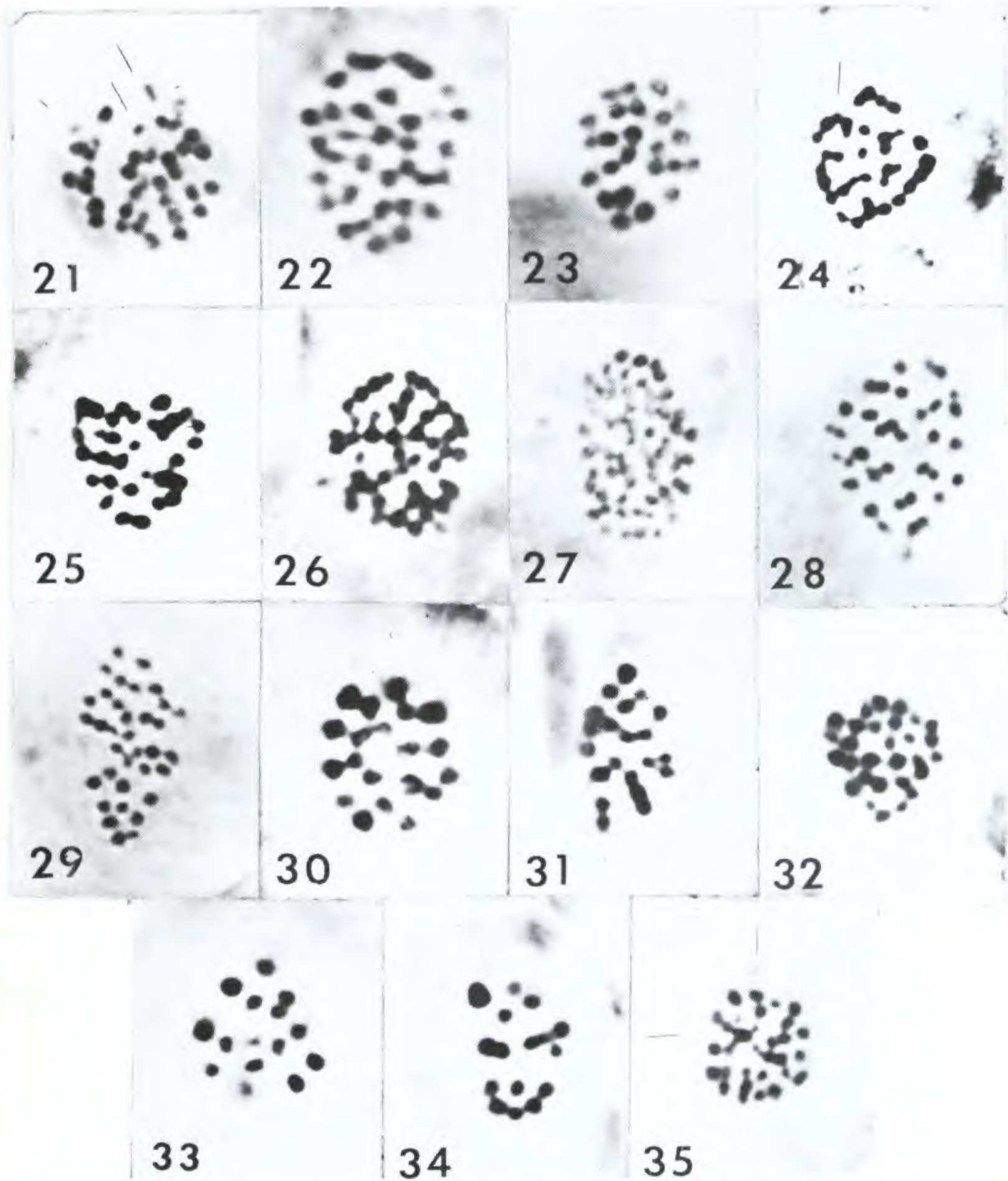
The chromosome numbers in 11 of 19 species of section *Pachysedum* are also  $n = 34$ , and it is likely that the evolutionary connection between *Pachysedum* and other species of *Sedum* lies somewhere among the immediate ancestors of the *Sedum palmeri* group. Most genera of subfamily Echeverioideae also have the same or similar basic chromosome numbers (Uhl, 1970, 1976a, Uhl & Moran, 1973), and they may have originated from the ancestral genus *Sedum* as a further development from ancestors that would have been classified in Section *Pachysedum* (Uhl, 1978).

Vegetative axes in species of the *Sedum palmeri* group are continued beyond the terminal inflorescences by branches which develop from the axils of leaves a few nodes below the inflorescence. Sometimes, after flowering, growth of the axillary vegetative axis pushes aside the terminal inflorescence so that the latter superficially appears to be lateral. In some members of section *Pachysedum* (e.g., *S. praealtum*, *S. cremnophila*) the lateral vegetative and

inflorescence axes are not all distinguishable when young, and commitment of a branch to remain vegetative or to become an inflorescence is not immediately apparent. From ancestors similar to the *S. palmeri* group evolution of lateral inflorescences characteristic of section *Pachyseudum* (and also of subfamily Echeverioideae) could be accomplished by maintaining only vegetative growth in the meristem of the main axis while only certain lateral axes (probably determined by seasonal factors) become committed to produce inflorescences.

*Sedum obcordatum* Clausen ( $n = 34$ , one collection, Fig. 18) is readily distinguished from *S. palmeri* by its decussate leaves and erect petals, but the chromosome numbers are the same. It occurs at high elevations on Cofre de Perote and Citlaltepétl (Orizaba) on the boundary between the states of Puebla and Veracruz (Clausen, 1959). A hybrid with *S. cremnophila* ( $n = 33$ ) of section *Pachyseudum* (= *Creemnophila nutans*) ( $U1583 \times M10174$ ) shows the greatest proportion of chromosome pairing seen in any hybrid between species with terminal and with lateral inflorescences—30–33 bi- and multi-valents and 0–6 univalents in 12 cells analyzed—but it produces no stainable pollen (Uhl, 1976a). Surprisingly, a hybrid with *S. platyphyllum* ( $n = 29$ ) of section *Centripetalia* (q.v.) ( $M7737 \times U1583$ ) also shows mostly bivalent pairing at metaphase I. *Sedum obcordatum* has also been crossed with the cytologically variable *S. greggii* ( $n = 33$ ) and with *Graptopetalum fruticosum* ( $n = 31$ ), *Villadia grandisepala* ( $n = 44$ ), *S. craigii* ( $n = 30$ ), and *Pachyphytum hookeri* ( $n = 32$ )—the two last have not yet flowered. Forty-nine other attempts have yielded no hybrids. Three of the unsuccessful attempts were with *S. palmeri*, and these two species may not really be as closely related as their grouping together here implies.

*Sedum palmeri* S. Watson occurs on the eastern slopes of the Sierra Madre Oriental from the vicinity of Monterrey southeast beyond Ciudad Victoria, Tamaulipas. Plants from the northern part of the range, including a near topotype ( $U1367$ ), are all diploids, with  $n = 34$  (ten collections, Fig. 19) or  $n = 35$  (one collection), but most plants from southwestern Tamaulipas, including a topotype of *S. compressum* Rose, are tetraploids ( $n = 68$ , 9 collections, Fig. 20). Most tetraploids are a bit smaller than most diploids, but the differences seem not sufficient to warrant status as a separate species.



Figures 21–35. Chromosomes of *Sedum* at metaphase I in pollen mother cells,  $\times 2000$ . Thin lines point to univalents or B-chromosomes. 21, *S. cf. palmeri*, M7658,  $n = 34 + 3B$ ; 22, *S. torulosum*, UC54.234,  $n = 34$ ; 23, *S. botteri*, 6A,  $n = 24$ ; 24, *S. burrito*, U2073,  $n = 34 + 1$ ; 25–27, *S. calcicola*; 25, M13368,  $n = 32$ ; 26, M7816,  $n = 48$ ; 27, M10046,  $n = 64$ ; 28, *S. furfuraceum*, M7659,  $n = 34$ ; 29, *S. morganianum*, U1270,  $n = 35$ ; 30–31, *S. quevae*; 30, SE3,  $n = 20$ ; 31, M7767,  $n = 21$ ; 32, *S. stahlii*, M2129,  $n = 29$ ; 33–34, *S. tortuosum*; 33, UC58.830,  $n = 15$ ; 34, M7620,  $n = 16$ ; 35, *S. retusum*, M7811,  $n = 31 + 1 + 1B$ .

On the other hand, two plants from still farther south, in eastern San Luis Potosi and eastern Guanajuato, on the western ranges and slopes of the Sierra Madre Oriental system, have thicker, whiter leaves borne in much looser rosettes than the others. These plants also have  $n = 34$  (one of them with B-chromosomes, Fig. 21), but are worth consideration as a new species.

Diploid *Sedum palmeri* has been crossed with three species of section *Pachysedum*, *S. craigii* ( $n = 30$ ), *S. cremnophila* ( $n = 33$ ), and *S. sp. nov.* (UC58.858,  $n = 34 + 1$ ), and with two species of subfamily Echeverioideae, *Echeveria derenbergii* ( $n = 27$ ) and *Pachyphytum hookeri* ( $n = 32$ ), and also with *Villadia nelsonii* ( $n = 20$ ). Thirty-eight other attempted crosses involving 28 other species gave no progeny. Tetraploid *S. palmeri* (= *S. compressum*) has given no progeny after attempted crosses with three other species. The anomalous diploid from San Luis Potosi and Guanajuato has been crossed with *Graptopetalum fruticosum* ( $n = 31$ ), but attempts with five other species were unsuccessful.

*Sedum torulosum* Clausen ( $n = 34$  in a clonotype, Fig. 22) forms plants up to a meter tall, with knobby stems up to 10 cm. or more in diameter at the base. Originally described from cultivated material of uncertain origin, it is now known to occur in northwestern Oaxaca. In many years of cultivation at Ithaca it has never flowered, although it does so profusely outdoors in California. Using flowering material brought from California, *S. torulosum* has been crossed with two species of section *Pachysedum*, *S. clavatum* and *S. cuspidatum*, and with two members of subfamily Echeverioideae, *Graptopetalum fruticosum* and *Pachyphytum hookeri*. None of these has yet flowered. Attempted crosses with *S. frutescens* and *S. lucidum* yielded no progeny.

#### MISCELLANEOUS SPECIES.

Some other more or less shrubby species are listed here alphabetically. However, their affinities with each other and with the species and groups listed previously are not clear, either on cytological or on morphological grounds, or both. Probably at least some of them are more closely related to one or another of the more herbaceous species of *Sedum* than they are to other shrubby or subshrubby species.

*Sedum botteri* Hemsley ( $n = 24$ , three collections, Fig. 23) is usually epiphytic, with rather large, obovate or oblanceolate leaves and greenish flowers, speckled with reddish. It ranges from Veracruz to Chiapas. Clausen (1959) considered it most closely related to *S. tortuosum* ( $n = 15$  and  $16$ ) and to be relatively unspecialized, possibly "most like the ancestral stock from which various other groups of species have evolved." However, its chromosome number is unique among all the woody Mexican species of *Sedum*, and this suggests that it may not be closely related to any of them.

The recently described *Sedum burrito* Moran (1977) has pendent stems like the very similar *S. morganianum*, but its floral parts and leaves are shorter and blunter, and the leaves are more spreading. No definite locality is yet known for it in the wild, but, like *S. morganianum*, it is suspected that it may be native somewhere on the eastern slopes of Mount Orizaba or nearby (Moran, 1977). Two plants obtained from cultivation at widely separated places in Mexico both have 35 chromosomal elements at metaphase I (Fig. 24), as does *S. morganianum*, but in both collections of *S. burrito* one element consistently is a univalent, and at anaphase I a laggard is usually seen. It is not clear whether these plants are monosomics ( $2n-1$ ) based on  $n = 35$  or trisomics ( $2n+1$ ) based on  $n = 34$ . Study of field-collected plants may be necessary to determine whether the normal chromosome numbers of *S. burrito* and *S. morganianum* are the same, but no such plants are yet known for either species. Most (all?) inflorescences of *S. burrito* are definitely lateral, and the species perhaps should be assigned to section *Pachysedum*. Its chromosome number is compatible with this.

Hybrids of *Sedum burrito* have been produced with *S. morganianum*, with *S. lucidum* of Section *Pachysedum* and with two species of subfamily Echeverioideae, *Graptopetalum fruticosum* and *Pachyphytum hookeri*. Crosses with three other species were unsuccessful.

*Sedum calcicola* Robinson and Greenman is an older name for the species better known as *S. lenophylloides* Rose (Clausen, 1978). It occurs in the Sierra Madre Oriental from the vicinity of Monterrey south to the state of Hidalgo. The 13 collections studied represent three levels of ploidy, with a presumed basic chromosome number, not yet found, of  $x = 16$ , but the relationship, if any, between polyploidy and distribution is not clear. The northernmost

collection (U1370), which is a near topotype of *S. lenophylloides*, and also the southernmost (M10046) and three others were all octoploid ( $n = 64$ , Fig. 27). Tetraploids ( $n = 32$ , Fig. 25), including a near topotype of *S. calcicola* (U1646), were widely distributed in the interior of the range (six collections, four localities), and two hexaploids ( $n = 48$ , Fig. 26) came from probably the same population in north central San Luis Potosi.

*Sedum furfuraceum* Moran ( $n = 34$  in a plant of the type collection, Fig. 28) forms mats with thick, fleshy, creeping stems and small, egg-shaped leaves with a scaly cuticle. Its type (and only) locality is near Zaragoza, San Luis Potosi (Moran, 1961). A cross with *S. greggii* ( $n = 33$ ) yielded a single hybrid (M7807  $\times$  M7659), but 12 other attempted crosses produced nothing. Its chromosome number is common in Mexican *Sedum*, but the species seems not closely related to any others.

*Sedum morganianum* Walther, the "donkey's tail", has  $n = 35$  (Fig. 29) in three collections, all from cultivation and possibly all the same clone, but including one traceable back to the type collection. The species is popular and very widely cultivated in Mexico and elsewhere, but no definite locality is known for it in the wild. Rumors of possible wild populations near the eastern slopes of the peak of Orizaba have not yet been confirmed (Moran, 1977).

This species has pendent stems with blue-glaucous leaves and deep pink, erect petals. Its woody stems and thickened, subterete leaves and its erect petals resemble those of some species of section *Pachysedum* (e.g., *Sedum corynephyllum*,  $n = 34$ ), and its chromosome number is similar. The inflorescences are terminal on the pendent shoots, which arise laterally from a crowded basal branching system, and which rarely or never branch before flowering. *Sedum morganianum*, along with the very similar *S. burrito*, should perhaps be assigned to section *Pachysedum*.

Attempts to cross *Sedum morganianum* with three species of section *Pachysedum* have been unsuccessful, but the species has been crossed with *S. burrito* and *S. platyphyllum* and with nine species of subfamily Echeverioideae (in 25 attempts): *Echeveria ciliata*, *E. cuspidata*, *E. walpoleana*, *Graptopetalum amethystinum*, *G. fruticosum*, *Pachyphytum compactum*, *P. hookeri*, *P. kimnachii*, and *P. viride*. Chromosome pairing in some of these hybrids is not so nearly complete as it is in most hybrids within or between section *Pachysedum* and subfamily Echeverioideae, but it is more extensive

than in most other hybrids. *Sedum morganianum* and *S. burrito* may have evolved from the same ancestral stocks in parallel with section *Pachysedum* and perhaps also with the *S. palmeri* group.

*Sedum quevae* Hamet has oblanceolate leaves and tuberous roots. It occurs from Morelos and Tlaxcala to Oaxaca. Collections from four northern localities all had  $n = 20$  (Fig. 30), but plants from two localities in Oaxaca had  $n = 21$  (Fig. 31). *Sedum quevae* has the morphological characters of section *Fruticisedum*, to which Jacobsen (1974) assigned it, but its very different chromosome numbers raise doubt that it truly belongs there. Tuberous roots also occur in most species of *Villadia*, and Clausen (1959) reported two natural hybrids between *S. quevae* and *V. scopulina*. Recent crosses with *S. oxycoccoides* resulted in three seedlings and with *S. bourgaei* in ten seedlings. Parentage of these seedlings has not yet been confirmed. A cross with *S. palmeri* was unsuccessful.

*Sedum stahlii* Solms has leaves that are terete, puberulent, decussate and usually strongly flushed with red, and it has bright yellow petals each with a subapical mucro. It occurs mostly in the area between Tehuacan, Puebla, and Orizaba, Veracruz. Although its chromosome number ( $n = 29$ , five collections, Fig. 32) is the same as in many other woody Mexican sedums, its affinities are not clear. Perhaps it is closest to *S. allantoides* of section *Centripetalia*, which also has  $n = 29$ , thickened, subterete leaves, and petals with a subapical mucro. An attempt to cross these two was unsuccessful, but a hybrid was obtained of *S. stahlii* with *S. platyphyllum* ( $n = 29$ ), which is very closely related to *S. allantoides* ( $M7737 \times U1460$ ). This hybrid showed very irregular meiosis that defied precise analysis, with more univalents than paired elements in most cells at metaphase I, indicating that the chromosomes of the parental species have only relatively scant and weak homology for each other.

Hybrids of *Sedum stahlii* with *S. cuspidatum* ( $n = 34$ ) and with *S. cremnophila* ( $n = 33$ ), both members of section *Pachysedum*, and also with *Graptopetalum fruticosum* ( $n = 31$ ) of subfamily Echeverioideae also show more univalents than paired elements at metaphase I. Attempted crosses with eight other species were unsuccessful.

The subapical mucro on the petals of *Sedum stahlii* appears in reduced form in its hybrids. It also is seen on petals of *S. \times rubrotinctum*, which appears to be a garden hybrid having *S. stahlii* as one parent and probably *S. pachyphyllum* ( $n = 34$ ) of section

*Pachysedum* as the other (Uhl, 1978). A single seedling resulted from a cross between these two species but died without flowering.

*Sedum tortuosum* Hemsley is usually epiphytic, with winged seeds attached to nearly basal placentas (Clausen, 1959). Plants from two localities in Durango and Jalisco had  $n = 16$  (Fig. 34). These may correspond to *S. lignicaule* Fröderström, but Clausen (1959) reduced that species to *S. tortuosum*. Plants from three localities in Oaxaca all had  $n = 15$  (Fig. 33), one of them usually with univalents (precociously separated bivalents?) at metaphase I. Clausen thought *S. tortuosum* most closely related to *S. botteri* ( $n = 24$ ) and to *S. guatemalense* ( $n = 27$ ), but the chromosomes are very different. *Sedum tortuosum* was listed in section "*Frutisedum*" by Jacobsen (1974), but its chromosomes differ significantly from those of other species in that section, as it is delimited here. Six attempts at hybridizing *S. tortuosum* (U2063,  $n = 16$ ), involving four other species of *Sedum*, were unsuccessful.

*Sedum tuberculatum* Rose of southern Oaxaca has  $n = 16$  (one collection). Jacobsen (1974) classed this species in his section "*Frutisedum*", but the chromosome number suggests that it may not be closely related to the species of that section, as it is conceived here, which have  $n = 29$ , more or less.

### Summary

Chromosome numbers are reported for 127 collections representing at least 24 more or less woody species of Mexican *Sedum* having terminal inflorescences. Nine species have  $n = 29$ , six have  $n = 34$ , and the others have from  $n = 15$  to  $n = 68$ . One species is tetraploid and four others include polyploid races. Five other species have dysploid chromosome races, and some plants of three species have unpaired and/or B-chromosomes. Cytologically and morphologically these species fall into at least three groups, plus a number of miscellaneous species, some of which may be more closely related to various non-woody species: (1) Section *Centripetalia*, with two closely related species, both  $n = 29$ ; (2) Section *Fruticisedum*, with ten species,  $n = 26$  to 31 or a multiple, including six species with  $n = 29$ ; (3) the "*Sedum palmeri* group", with three or four species, all with  $n = 34$  or 68, and (4) a miscellaneous group of nine species, several of which are quite different cytologically from all the others, with  $n = 15, 16, 20, 21, 24, 29, 32, 34, 35, 48$  and 64.



Although these species resemble section *Pachysedum* in their woody habit, with several possible exceptions they seem to be not closely related to that section. This conclusion is based on the contrast between the relative difficulty of hybridizing almost any one of these species with a species of section *Pachysedum* and especially on the more limited chromosome pairing observed in most hybrids so obtained, compared with a usually much greater ease of hybridizing two species of *Pachysedum* with each other and a much more extensive pairing among the chromosomes in such hybrids. The same kind of evidence also suggests that, among the species reported here, *Sedum palmeri* and *S. obcordatum* (both  $n = 34$ ), and also *S. moranianum* ( $n = 35$ ) and *S. burrito* ( $n = 34+1$ ), are probably the ones that are most closely related to section *Pachysedum* and to the common ancestral stocks.

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